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INVITATION PAPERS AT THE BALTIMORE MEETING OF THE BOTANICAL SOCIETY OF AMERICA

AT the recent Baltimore meeting of the Botanical Society of America, three series of special papers were read by members who were specially requested by the council of the society to prepare them for the occasion.

The first set of papers dealt with certain phases of recent advance in our knowledge of vascular anatomy in plants. These papers, read on December 29, were by J. M. Coulter and E. C. Jeffrey.

The papers of the second series were read at a symposium on "Present Problems in Plant Ecology," on Wednesday, December 30. The participants were H. C. Cowles, B. E. Livingston, C. H. Shaw, V. M. Spalding and E. N. Transeau.

The papers of the third series were read at the Darwin Memorial Session, held on Thursday, December, 31. These addresses gave estimates of Darwin's work in three fields of botanical investigation. The participants were Wm. Trelease, F. E. Clements and H. M. Richards.

In accordance with the instructions of the society, all of the above mentioned papers are here published in full.

DUNCAN S. JOHNSON,
Secretary.

OFFICE OF THE SECRETARY,
BALTIMORE, MD., February 1, 1909.

DARWIN MEMORIAL SESSION

In response to a letter announcing the plans for the Darwin Memorial Session, and suggesting that some

word of greeting on that occasion would be very appropriate, and pleasing to his botanical colleagues in America, Professor Francis Darwin sent the following letter to the president of the Botanical Society of America. It arrived, unfortunately, for a reason stated in the letter, too late for the meeting, but it obviously belongs with the other contributions thereto.

13, Madingley Road, Cambridge. Dec. 23, '08.

Dear Sir;

Owing to absence from home I am only now able to answer your very kind letter. I am afraid my answer can not reach you in time, which I much regret. I should have liked to express thro'h you as president my sympathy with this assembling of American botanists to honour my father's memory. It is a source of sincere satisfaction to me to know that such a meeting is to be held. I am reminded of my father's words to Asa Gray:

"Hooker has forwarded to me your letter to him; and I can not express how deeply it has gratified me. To receive the approval of a man whom one has long sincerely respected, and whose judgment and knowledge are most universally admitted, is the highest reward an author can possibly wish for."

Your meeting is a posthumous "reward," and though I have no right to speak for English botanists I know that they will appreciate it as it deserves.

Yours sincerely,
Francis Darwin.

DARWIN AS A NATURALIST: DARWIN'S WORK ON CROSS POLLINATION IN PLANTS

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CHARLES DARWIN is rated as a great man, and there are really not many to-day who would dispute his title to this verdict; but he did not come easily to it.

In botany, he never did a thesis on morphology or cytology, or photosynthesis; he was puzzled rather than deranged by nomenclature; the reason that he provided for the compilation of an index to the names and authorities of all known flowering plants and their countries, in a way, is a confession that he was not a taxonomist; and a really fair all-round doctor's examination, with botany as a major, would have been likely to give him more than the proverbial trouble. He does not seem to have considered himself a botanist, and perhaps has never been admitted to the fraternity formally—though he has opened our eyes to some of the most interesting aspects of plant physiology, baring their secrets in a masterly way with the rough-and-ready direct methods and apparatus of an adept.

His earlier publications were on geology and zoology. My impression is that botanists—aside from the very few who know—looked on him in his lifetime rather as a zoologist. And yet even to-day amusement may be derived from reading what has been made public of the debate before the French Academy, when his name was under discussion for membership in the zoological section of that great body and one of the immortals was ready to place a hundred zoologists before him because of their contributions of demonstrable facts to the science.

The greatness of the man itself long stood in the way of its recognition. He had not classed himself with suffi-

cient minuteness in the subdivision of science. Looking back on his career, it is not difficult to see that the geological problems opened up to him by the voyage of the "Beagle" would have afforded an interesting field for detailed life work in geology which would have placed him quickly among the foremost geologists of his day if he had devoted himself to them and continued to publish on that subject and for those specialists. Even the French savants saw in his barnacle studies the work of far more than a tyro; but he did not choose to devote himself to the morphology and classification of animals. So little had he been thought of generally as knowing anything of botany, that the *Gardeners' Chronicle* reviewer of his orchid book expressed himself as doubly constrained to care in critically analyzing it. He was somewhat like a versatile witness questioned individually by the members of a polyglot jury, each using and understanding his own language and getting nothing more than a minute fragment of the whole testimony: he can hardly be said to have had a hearing before his peers—of whom it would have been hard, even, to draw a full panel at any time in the world's history.

Darwin was really a philosopher. His son speaks of him as seeming to be so charged with a theorizing power that no fact, however small, could avoid releasing a stream of theory which itself magnified the fact in importance; but just enough to his theories not to condemn them unheard, so that he was willing to test what would seem to most people not at all worth testing. This is at once the key note to his life work and his greatness in influencing human thought. Though his philosophy has received unusual, and perhaps undue, attention, through clashing with some of what had become incorporated in the theology of his day, his service in molding our way of seeing nature may be coordinated with that of the great men who have reduced the movements of the planets to a physical basis and the transmutations of matter to terms of chemistry.

Curiously, the human mind of the twentieth century does not seem to be superior as a reasoning machine to that of the time of the Greeks, and it is not surprising that the general conclusions of Darwin's philosophy had been reached in one form or another all the way along the past three thousand years. That his name goes into history as their father, results from the way in which he arrived at and substantiated them rather than from their novelty: his greatness in great thought is the natural achievement of a large mind reaching its ends by way of the painstaking study of little things.

So full a discussion of Darwin from many points of view is provided in the symposium of our fellow society, the American Association for the Advancement of Science, and in the allotment of subjects for our own Darwin-session, that I should use time to little advantage if I were to go into illustration of this, outside the special field assigned me on the program—to the discussion of which I have been asked to preface this general introduction.

I wish that I might quote Darwin's first utterance on the subject that has been assigned specially to me for this meeting, but I do not know where to find it. In his autobiography, he states that in 1838 or 1839 he had begun to attend to the cross fertilization of flowers by means of insects, from having come to the conclusion in his speculations on the origin of species, that crossing played an important part in keeping specific forms constant. Even then he had noticed the floral dimorphism of *Linum*. In the preface to his book on the fertilization of orchids he explains that its publication resulted from the criticized exclusion (because of lack of space) of detailed facts substantiating an opinion expressed in his work on the origin of species, that it is apparently a universal law of nature that no hermaphrodite fertilizes itself for a perpetuity of generations—a law which he has stated in a variety of other phrases, and the suggestion of which he owed to Knight. The introductory

chapter of his book on the effects of cross and self-fertilization in the vegetable kingdom indicates that this conclusion, based on his personal observations on plants, was guided to a certain extent by the experience of breeders of animals (which is detailed at length in his book on the variation of animals and plants under domestication).

It was, therefore, not a novice who entered the botanical field when, in October, 1857, Darwin contributed a one-column note to the *Gardiners' Chronicle* on bees and fertilization of kidney beans, which he was attracted to through "believing that the brush on the pistil, its backward and forward curling movement, its protrusion on the left side, and the constant alighting of the bees on the same side, were not accidental coincidences, but were connected with, perhaps necessary to, the fertilisation of the flower." His subsequent papers and books, vivifying floral ecology, were therefore as inevitable from one who was moved by a new teleology in natural science as was the superb publication of a half century earlier by Sprengel, who, seeing the petal-hairs of a Geranium, sought after their meaning in the firm conviction that the wise Author of nature had not created even a hair in vain.

Darwin's publications in this field are not numerous; omitting abstracts and reprints of papers published in full, and later editions and translations, they number only twenty-two.[1] They are remarkably direct in purpose, simple in treatment, clear in reasoning, and free from a controversial or dictatorial spirit. His own observations and experiments were rarely accepted at their face value, but were checked up with rather unusual care; and, as we now know from his published letters, his conclusions were commonly subjected to the criticism of a very select private audience before going to the world at large.

The comprehensiveness of the studies underlying these publications may be indicated by the statement that

[1] See bibliography at end.

nearly 350 genera of plants, represented by about 600 species (several of them in a number of contrasted forms and varieties), are made the subject of comment. No insignificant proportion of this large number were under observation or experimental cultivation through a considerable number of years—the series on which the "Cross and Self-Fertilization" volume was based having been grown in numbers and with painstaking care through more than a decade; and the plants measured and the seeds counted were very many. No observer was so insignificant that his observations escaped analysis if they came to the knowledge of the great naturalist, though Darwin was sorely tried by the positive statement of some non-existent facts; and some of the prettiest workings of his mind are shown in the elimination of untenable conclusions which had been drawn by predecessors whose observations were recorded in sufficient detail to permit another to winnow them afresh. Enthusiasm in fitting his own observations into his theories occasionally led to error when facts were scanty or incompletely made out, but in such cases these were usually employed with a word of caution and errors were eliminated with a charming candor when discovered subsequently; and few writers have more gracefully accepted rectifications by others—even when bluntly phrased or embodied in aggressive criticism, as was sometimes the case.

First, last and always, his studies were directed to the species question, but in his pollination studies, as in every other field that he entered, he bent himself to collateral details with the zeal of a specialist. He was never oblivious to the treacherous frailty of small numbers and few series; but his innate soundness of judgment was checked and confirmed, here and there, through the rehandling of his data by one to whom the analysis of figures was a specialty. The dainty instruments of precision in the use of which physiologists train their undergraduate students, were neither used nor desired by him;

but his experiments were devised with very unusual expertness and, like his figures, made to reveal their own defects and reenforce one another as indicating directions of high probability even where they were seen to stop far short of proof.

The problems which Darwin here set before himself for solution were primarily the explanation of natural phenomena—most of which others had observed in a general way—which in his belief could not be meaningless. Though doubtless not his first essay, his first publication on the subject, in 1857, primarily stated observed facts in *Phaseolus* and attacked them in this spirit, but incidentally he analyzed the reasons why and how bees visit flowers and what their intelligence is, and faced the broad question why varieties of beans do not freely mix if their flowers are really so formed as to secure frequent intercrossing. The behavior of introduced plants separated from their natural pollinators, further came into the next paper, with a distinct enunciation of Knight's law. Why Vincas do not seed; what their pollinators are; the details and meaning of what Dr. Gray has called heterogony, understanding which gave him unparalleled satisfaction; why flowers of two or even three nominal genera should sometimes appear on one plant of *Catasetum;* the substantiation of Knight's law by detailed arguments of adaptation selected from a single family of plants; the reason why *Lythrum salicaria* is represented by three sets of individuals as distinct from each other in floral characters as if they belonged to different species, and incidentally why *Lagerstræmia* should possess a (less clearly analyzed) stamen-variability; why the wild oxlip should be held for a hybrid between other closely related primroses and why these are specifically distinct; an extensive experimental testing of the utility underlying Knight's law; and a comparative analysis of heterogony, sex-separation, and cleistogamy: these were the questions set for answer in subsequent publications.

The methods by which the problems were attacked were neither many nor complicated. Patience and forethought and perseverance are their chief characteristics. Observation, not exclusive of any discernible fact; experimentation, with control of the incidental results of manipulation; testing the parent condition of seeds supposed to be pure; consideration of alternative explanations of phenomena, and especially of those opposed to the conclusions adopted; counting, weighing, measuring —almost beyond belief; ingenious substitutions for insects in laboratory and garden observations on structures concerned in pollination; watching insects at work on flowers and supplementing such observation by notation of the record of their visits afforded by the flowers themselves; confirming the identity of doubtful pollinia on a moth by restoring their original color through moistening them; field observations at all hours and under all climatic conditions; ascertaining pollen-tube development in prepotency questions; painstaking pollinations to cover numerous permutations: such were the methods.

The results of Darwin's work in this field are not easily epitomized. It is not going too far to say that he secured universal recognition of Sprengel's unheeded demonstration that the structure of many flowers serves to ensure their pollination by unconscious insect aid; he broadened this by enough detail to warrant the conclusion that in general it serves to ensure cross-pollination by such aid, in this way substantiating Knight's law "nature intended that a sexual intercourse should take place between neighboring plants of the same species"; he gave experimental demonstration of the benefits of crossing, not in itself, but through the interbreeding of individuals which for several generations have been subjected to slightly different conditions, or as he puts it, to "what we call in our ignorance spontaneous variation"; and he showed at once the utility of assured partial self-fertilization as

effected by cleistogamic degradation, the benefits of assured crossing resulting from the combined structural and physiological differentiation characteristic of heterogony, and the probability that complete sex-separation "did not commence and was not completed for the sake of the advantages to be gained from cross-fertilization" —but has rather to do with the general problem of division of labor.

His manner of presenting conclusions is at once interesting, convincing and charming. Egotism abounds in his writings; but the "I" and the "my" are not those of the man thinking in first-person pronouns, but of one unwilling to speak in a cathedratic manner and careful to state even obvious conclusions as merely the results to which he as an individual had been unavoidably led. He wrestled with thought synonymy even more earnestly than men now do with that of species; and, for instance, by his use of the word "fertilization," not infrequently compels the reader to take his perfectly unescapable meaning broadly and not too literally; and his inability to find better words to express the significance of floral structures than "adaptation" and "contrivance," reveals the deep basic idea of teleologic causation that the human mind has embodied in the machinery for uttering human thought. His phraseology is often aphoristic. For instance: "No one will understand the final cause of the structure of many flowers without attending to this point" [resultant crossing]; "Who would have been bold enough to surmise that the propagation of a species should have depended on so complex, so apparently artificial, and yet so admirable an arrangement?" [as that in Catasetum]; "A fortunate accident for the plants" [if the detention of moths in securing *Orchis* nectar, long enough for the pollinia to harden on to them were accidental]; "Nature abhors perpetual self-fertilization"; "Belief that flowers of any plant are habitually fertilized in the bud, or are perpetually self-fertilized, is a most

effective bar to really understanding their structure''; sexual differences may ''characterize and keep separate the coexisting individuals of the same species in the same manner as they characterize and have kept separate those groups of individuals, produced from common parents during the lapse of ages or in different regions, which we rank and denominate as distinct species''; ''Illegitimate unions [in heterogonous plants] are hybrids formed within the limits of one and the same species.''

Through it all, too, runs a thread of similar sentences revealing the soul of the man, groping only after the truth, to whom ''the whole subject is as yet hidden in darkness.'' In this spirit he lived, worked and wrote. Quite apart from success in accomplishing the direct purpose for which he worked, he succeeded to an exceptional degree in stimulating the research instinct in others, and directing it into attractive and prolific fields, seeing realized almost immediately his prediction that what had been held for trivialities might, when understood, ''exalt the whole vegetable kingdom in most persons' estimation.''

Things did not always go in his work as they were expected to—his first belief that if every bee in Britain were destroyed there would be no more pods on the kidney beans in that country, gave place to the certainty that a small percentage of fruit may set without such aid, and this particular species afterwards gave him less than the customary evidence of the benefits of crossing; but in general his expectation was sustained, or gave place to a better result for his general needs, and incidentally provided a wealth of detail consonant with his evolutionary theories and not yet known to be explicable on other grounds. Aside from this participation in his broader achievements, his work on floral ecology and fertilization, as has been said, has furnished one of the greatest stimuli of modern times to purposeful coordinated observation of minutiæ, not one of which is meaningless—in a field open to all who can see, whether or

not enjoying the privileges of great libraries and laboratories.

That he hovered very close to the edge of discoveries that were reserved for others, is clear to every one familiar with his publications. The effect of foreign pollen in modifying the seed (aside from the embryo) and fruit, was early known to him; but neither his studies nor those of others in his day were equal to the demonstration of double fertilization—even as to-day we go no further than the endosperm in accounting for these phenomena. Even his second botanical paper (1858) detailed at length a gardener's observations and his own experiments on a mongrel lot of beans which Darwin had the acuteness to test by growing some of the parent seed as well, and thus to demonstrate that this itself must have been crossed and not pure. Mendel's law—hardly deducible from these facts, but again suggested in his study of the heredity of style- and stamen-length in illegitimate unions of heterogonous species (which he contrasts with hybridization)—escaped him, and the obscurity of its publication seems to have prevented him from enjoying its benefits at all in his analysis of the complex problems of heredity. He was on the verge of knowing the important part that light sometimes plays in the phenomena of germination, but at most barely knew it. To him had not come the fundamental distinction between fluctuating and mutating variations; and the demonstration that cumulation of the latter and not accretion of the former underlies organic evolution was left for others—to whom the basal mystery of causation is likely long to remain as obscure as it confessedly was to Darwin. Convinced, beyond the possibility of doubt, of the benefits of sexual differentiation with attendant union of elements derived from different individuals, he paused before the question why this differentiation is beneficial up to a certain point and injurious if carried still farther; confessing in candor that he did not know what is the nature or degree of the differentiation, and

adding with characteristic humility that at the end he still stood in awe before the mystery of life.

Large as is his service to botany, even in the partial field assigned me on this program, it is but an incident in his life-long struggle with this great mystery on the border-line between the discoverable and the eternally unknowable.

DARWIN'S PUBLICATIONS ON POLLINATION AND FERTILIZATION

1. Bees and fertilisation of kidney beans. Gard. Chron. **1857**: 725.
2. On the agency of bees in the fertilisation of papilionaceous flowers, and on the crossing of kidney beans. Gard. Chron. **1858**: 828–9.—Ann. & Mag. of Nat. Hist. iii. **2**: 459–465.
3. The origin of species by means of natural selection: or the preservation of favored races in the struggle for life. London, 1859, etc. Index.
4. Fertilisation of British orchids by insect agency. Gard. Chron. **1860**: 528.—Entomol. Weekly Intelligencer. **1860**.
5. Fertilisation of Vincas. Gard. Chron. **1861**: 552.
6. Fertilisation of orchids. Gard. Chron. **1861**: 831.
7. Vincas. Gard. Chron. **1861**: 831–2.
8. On the two forms, or dimorphic condition, in the species of *Primula*, and on their remarkable sexual relations. Journ. Linn. Soc., Bot. **6**: 77–96.—Abst. in Gard. Chron. **1861**: 1048–9.
9. On the three remarkable sexual forms of *Catasetum tridentatum*, an orchid in the possession of the Linnean Society. Journ. Linn. Soc., Bot. **6**: 151–7.—Abst. in Gard. Chron. **1862**: 334–5.—Transl. in Ann. des Sci. Nat., Bot. iv. **19**: 204–255.
10. On the various contrivances by which British and foreign orchids are fertilised by insects, and on the good effects of intercrossing. London, 1862, etc.
11. On the existence of two forms, and on their reciprocal sexual relation, in several species of the genus *Linum*. Journ. Linn. Soc., Bot. **7**: 69–83.—Read Feb. 5, 1863.
12. On the sexual relations of the three forms of *Lythrum salicaria*. Journ. Linn. Soc., Bot. **8**: 169–196.—Read June 16, 1864.
13. On the character and hybrid-like nature of the offspring from the illegitimate unions of dimorphic and trimorphic plants. Journ. Linn. Soc., Bot. **10**: 393–437.—Read Feb. 20, 1868.
14. On the specific difference between *Primula veris*, Brit. Fl. (var. *officinalis* of Linn.), *P. vulgaris*, Brit. Fl. (var. *acaulis* Linn.), and *P. elatior* Jacq.; and on the hybrid nature of the common oxlip. With supplementary remarks on naturally produced hybrids in the genus *Verbascum*. Journ. Linn. Soc., Bot. **10**: 437–454.—Read Mar. 19, 1868.
15. The variation of animals and plants under domestication. London, 1868, etc. Index.

16. Notes on the fertilization of orchids. Ann. & Mag. of Nat. Hist. iv. 4: 141–159.
17. Fertilisation of *Leschenaultia*. Gard. Chron. Sept. 1871: 1166.
18. Fertilisation of the Fumariaceæ. Nature 9: 460.
19. The effects of cross- and self-fertilisation in the vegetable kingdom. London, 1876, etc.
20. The different forms of flowers on plants of the same species. London, 1877, etc.
21. Fertilisation of plants. Gard. Chron. n. s. 7: 246.
22. Fritz Müller on flowers and insects. Nature 17: 78.

DARWIN'S INFLUENCE UPON PLANT GEOGRAPHY AND ECOLOGY

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DARWIN dealt with plant geography only incidentally in connection with origin by descent. He was concerned chiefly with the bearing of migration upon community of origin, and consequently with the question of single and multiple origin of species. In his discussion of migration is found some consideration of barriers, endemism and isolation, but only in so far as these contribute to his main theme. On what might be called the ecological side proper, *i. e.*, the response of the individual, Darwin made his greatest contributions. Leaving apart his studies of pollination, movement and insectivorous plants, the ecologist must consider his fundamental work in variation and adaptation, together with his conclusions upon the questions inseparably connected with them, namely, competition, selection, inheritance of acquired characters and mutation.

In estimating Darwin's influence in all these matters, I have endeavored to keep in mind three view points: (1) his exact opinion upon each question, (2) his actual contribution to it, and (3) his share in our present knowledge of the subject, as well, perhaps, as his influence in shaping our present opinions where they do not rest on experimental knowledge. Several inherent difficulties have manifested themselves during this attempt. Chief among these is the impossibility of ascertaining what might be called the majority opinion of botanists, a difficulty aggravated by the fact that no two botanists would draw the same line between what is proved and what is merely held. In addition, Darwin's own views seem to have remained plastic to a degree not always evident in his most widely read books. This has brought the curious result that his earlier views have often had much the greater

influence in moulding opinion, while his later views are more in accord with scientific knowledge. Furthermore, it must be borne in mind that Darwin was the great apostle of origin by descent. It was his unique mission to bring the scientific world to accept this doctrine, a task of such magnitude that methods of origin, for the time at least, were relatively unimportant. In attempting to determine Darwin's actual contribution, one is confronted by the task of deciding how much credit is to be given to the discoverer of a new idea or principle, and how much to him who applies it and establishes it. It is fairly well known that Darwin was not the first to formulate the principle of evolution. Even in regard to natural selection, often accepted as distinctly Darwinian, Darwin himself has shown that he was anticipated by three other writers. Yet the fact remains that Darwin has contributed more to the foundations of biology than all of his forerunners.

A careful rereading of the "Origin of Species" and the "Variation of Animals and Plants under Domestication" has been found necessary to make Darwin's views emerge clearly from the mists of tradition and of recollection. It has seemed desirable also that he should himself speak in his own words, without the handicap of paraphrase and of the personal equation. Together with the manifest difficulty of making accurate and definite statements of the consensus of botanical opinion on mooted questions, this necessarily results in a more or less fragmentary and detached account of such a vast field.[1] Its value lies wholly in recalling to us Darwin's actual views without interpretation or emendation, so that each may determine for himself what part Darwin's work plays in his own views, and in botanical opinion as he sees it.

DISTRIBUTION

Darwin formulated three laws of distribution: (1) "Neither the similarity nor the dissimilarity of the in-

[1] The references given after the various excerpts are to the sixth edition (1872) of the "Origin of Species," and to the second edition (1875) of the "Variation of Animals and Plants under Domestication."

habitants of the various regions can be wholly accounted for by climatal or other physical conditions," (2) "barriers of any kind or obstacles to free migration, are related in a close and important manner to the differences between the productions of various regions," (3) "the affinity of the productions of the same continent, or of the same area, though the species themselves are distinct at different points and stations."[2] These scarcely need comment, for they arise clearly from the law of origin by descent. They are such an intrinsic part of the foundation of plant geography as to require an effort to recognize the fact that it was once necessary to formulate them.

Single and Multiple Origin

From the very nature of his task, Darwin was forced to assume that species were first produced at one spot. To-day the fact that the same species may arise at two or more distinct places merely strengthens the law of descent, but in Darwin's time this would have greatly increased the difficulty of supporting his doctrine by the evidence drawn from the distribution of plants. Darwin's views upon this question were far from uncertain, as the following excerpt indicates.

> It is obvious that the individuals of the same species, though now inhabitating distant and isolated regions, must have proceeded from one spot, where their parents were first produced. We are thus brought to the question which has been largely discussed by naturalists, namely, whether species have been created at one or more points of the earth's surface. Undoubtedly there are many cases of extreme difficulty in understanding how the same species could possibly have migrated from some one point to the several distant and isolated points where now found. Nevertheless, the simplicity of the view that each species was first produced within a single region captivates the mind. He who rejects it, rejects the *vera causa* of ordinary generation with subsequent migration, and calls in the agency of a miracle.[3]

This view seems to be little more than an inheritance from the special creationists. It doubtless reflects the prevailing opinion of Darwin's time, and probably is in

[2] "Origin," 2: 129.
[3] "Origin," 2: 135.

accord with the consensus of opinion at present. What the current opinion is can only be a matter of conjecture, but notwithstanding the proofs of multiple origin afforded by adaptation and mutation, it would seem that the majority of botanists and nearly all zoologists still adhere to the doctrine of single origin.

MIGRATION

Darwin's treatment of migration is limited to evidence of the possibility of distant and occasional migration as the explanation of the many puzzles of distribution. It is evident that his position in regard to single origin caused him to turn to migration as the necessary solution of all the problems of distribution. His attitude upon both questions is shown by the following statement:

> Whenever it is fully admitted, as it will some day be, that each species has proceeded from a single birthplace, and when in the course of time we know something definite about the means of distribution, we shall be enabled to speculate with security on the former extension of the land.[4]

His experiments upon the carriage of seeds and fruits by ocean currents and by birds, though necessarily crude and simple, are classic. They still serve to indicate one of the really fundamental points of attack in the detailed quantitative study of migration.

VARIATION

A brief summary of Darwin's views upon variation is an impossibility. Under the headings "Causes of Variation," "Habitat as Cause," "Use and Disuse," I have assembled his own statements to make clear his position. These seem to differ in some essentials from the views often ascribed to Darwin, or at least held by many who regard themselves as his followers. They appear to be more in accord with the views of the ecologist who looks to the habitat for the final explanation of all changes, than with the opinions held by biologists in general. They show Darwin to have been much more in sympathy with

[4] "Origin," 2: 140.

Lamarck and Saint-Hilaire than he was himself aware. He thus becomes the connecting link between these two great but less appreciated seers, and the investigators of to-morrow whose success will rest on the experimental study of the habitat as the primary cause.

Causes of Variation.

I have hitherto sometimes spoken as if the variations so common and multiform with organic beings under domestication, and in a lesser degree under nature—were due to chance. This, of course, is a wholly incorrect expression, but it serves to acknowledge plainly our ignorance of the cause of each particular variation.[5]

No doubt each variation must have its efficient cause, but it is as hopeless to discover the cause of each as it is to say why a chill or a poison affects one man differently from another. Even with the modifications resulting from the definite action of the conditions of life, when all or nearly all the individuals which have been similarly exposed, are similarly affected, we can rarely see the precise relation between cause and effect.[6]

We must . . . conclude that organic beings, when subjected during several generations to any change whatever in their conditions, tend to vary: the kind of variation which ensues depending in most cases in a far higher degree on the nature or constitution of the being, than on the nature of the changed conditions.[7]

Those authors that adopt the latter view—that variability must be looked at as an ultimate fact, would probably deny that each separate variation has its own exciting cause. Although we can seldom trace the precise relation between cause and effect, yet the considerations presently to be given lead to the conclusion that each modification must have its own distinct cause, and is not the result of what we blindly call accident.[8]

Habitat as Cause.

With respect to what I have called the indirect action of changed conditions, namely, through the reproductive system being affected, we may infer that variability is thus induced, partly from the fact of this system being extremely sensitive to any change in the conditions. Many facts clearly show how eminently susceptible the reproductive system is to very slight changes in the surrounding conditions.[9]

Changed conditions of life are of the highest importance in causing variability, both by acting directly upon the organization, and indirectly by affecting the reproductive system. It is not probable that variability is an inherent and necessary contingent under all circumstances.[10]

[5] "Origin," 1: 164. [6] "Variation," 2: 273.
[7] "Variation," 2: 229. [8] "Variation," 2: 232. [9] "Origin," 1: 10.

These several conditions alone render it probable that variability of every kind is directly or indirectly caused by changed conditions of life. Or, to put the case under another point of view, if it were possible to expose all the individuals of a species during many generations to absolutely uniform conditions of life, there would be no variability.[11]

We have good reason to believe, as shown in the first chapter, that changes in the conditions of life give a tendency to increased variability, and in the foregoing cases the conditions have changed, and this would manifestly be favorable to natural selection, by affording a better chance of the occurrence of profitable variations.[12]

Use and Disuse.

It is notorious, and we shall immediately adduce proofs, that increased use or action strengthens muscles, glands, sense-organs, etc., and that disuse, on the other hand, weakens them.[13]

There can be no doubt that with our anciently domesticated animals, certain bones have increased or decreased in size and weight owing to increased or decreased use. With animals living a free life and occasionally exposed to severe competition, the reduction would tend to be greater, as it would be an advantage to them to have the development of every superfluous part saved.[14]

COMPETITION

In spite of the importance Darwin assigned to competition, for to him it usually comprises the whole process of natural selection, he gave little thought to its analysis and almost none to its investigation. His ideas of competition were drawn largely from Lyell and Herbert, and he was content to take it as a universal and fundamental process among living things, without detailed inquiry into its working or its precise relation to the origin of new forms. Darwin's actual contribution rests chiefly upon his formulation of the following law of competition, which recent quantitative experiments indicate to be fundamental:

As species of the same genus usually have, though by no means invariably, much similarity in habits and constitution, and always in structure, the struggle will generally be more severe between them if they come into competition with each other, than between the species of distinct genera.[15]

[10] "Origin," 1: 49.
[11] "Variation," 2: 234.
[12] "Origin," 1: 100.
[13] "Variation," 2: 276.
[14] "Variation," 2: 280.

Competition has, however, been almost completely neglected until the ecologist has begun the investigation of it in the last few years, and there are few subjects in which botanical opinion is so completely unformed.

Inheritance of Acquired Characters

Darwin's opinions upon this subject appear to have been modified little with time, contrary to the case with other views. Here again he was in almost complete accord with Lamarck and Saint-Hilaire, but he seems to have had little effect upon current opinion, especially among zoologists. The experimental ecologist would doubtless follow Darwin in regarding the inheritance of acquired characters as proved beyond question. Indications are not lacking that more and more botanists are coming to the same point of view. Darwin's attitude may be summed up in the following:

The increased use and disuse of various organs produces an inherited effect.[16]

With plants, the period of vegetation is easily changed, and is inherited, as in the case of summer and winter wheat, barley and vetches.[17]

Changed habits produce an inherited effect, as in the period of the flowering of plants when transplanted from one climate to another.[18]

Habit is hereditary with plants, as in the period of flowering, in the time of sleep, in the amount of rain requisite for seeds to germinate, etc.[19]

Perhaps the correct way of viewing the whole subject would be to look at the inheritance of every character whatever as the rule, and non-inheritance the anomaly.[20]

Mutation

Darwin's attitude towards the sudden appearance of striking variations, of sports, and monstrosities towards what is now called mutation, is one held by the majority of American botanists to-day. To the latter, DeVries has supplied the scientific proof of origin by sudden and striking variation, but only a small number, the followers of DeVries, regard mutation as the fundamental or uni-

[16] "Origin," 1: 93.
[17] "Variation," 2: 285.
[18] "Variation," 2: 273.
[19] "Origin," 1: 173.
[18] "Origin," 1: 12.
[20] "Origin," 1: 15.

versal process. Zoologists, it would seem, incline to look with greater favor upon mutation as the regular method of origin.

At long intervals of time, out of millions of individuals reared in the same country and fed on nearly the same food deviations of structure, so strongly pronounced as to deserve to be called monstrosities, arise; but monstrosities cannot be separated by any distinct line from slighter variations. All such changes of structure, whether extremely slight or strongly marked, which appear amongst many individuals living together, may be considered as the indefinite effects of the conditions of life on each individual organism.[21]

Some naturalists have maintained that all variations are connected with the act of sexual reproduction, but this is certainly an error: for I have given in another work a long list of "sporting plants," plants which have suddenly produced a single bud with a new and sometimes widely different character.[22]

Some variations useful to man have probably arisen suddenly, or by one step.[23]

No one supposes that our choicest productions have been produced by a single variation from one stock.[24]

It may be doubted whether sudden and considerable deviations of structure such as are occasionally seen in our domestic productions, more especially with plants, are ever permanently propagated in a state of nature.[25]

I saw also that the preservation in a state of nature of any occasional deviation of structure, such as a monstrosity, would be a rare event, and that if first preserved, it would generally be lost by subsequent intercrossing with ordinary individuals.[26]

ADAPTATION

Darwin recognized the three fundamental methods of origin in nature, namely, variation, mutation and adaptation. It seems probable that to mutation he assigned its approximate value. In the "Origin of Species," variation with selection was given the preeminent place, and adaptation a minor one. Later, adaptation assumed greater importance to his mind, and there is some evidence that he may have assigned to it a value greater than that of variation. He had come to see more clearly that natural selection operated upon things already produced,

[21] "Origin," 1: 9.
[22] "Origin," 1: 11.
[23] "Origin," 1: 34.
[24] "Origin," 1: 37.
[25] "Origin," 1: 52.
[26] "Origin," 1: 111.

and to catch a glimpse of the fact that indefinite action, *i. e.*, variation, and definite action of the habitat, *i. e.*, adaptation, were at bottom the same thing.

His changing view point is recorded in his letters, and hence his later views are not generally known. As a result, scientific opinion has been more or less stereotyped in the well-known statements of the "Origin of Species" and has maintained in greater or less degree a position which Darwin himself had forsaken. Darwin's later opinions upon adaptation, as upon the causes of variation, and upon the inheritance of acquired characters, did not differ essentially from those of Lamarck. More important than this, for Lamarck was a prophet, not an investigator, they are in accord with the first results of the application of exact ecological methods to the question of the origin of new forms in natural habitats.

As far as I am able to judge, after long attending to the subject, the conditions of life appear to act in two ways—directly on the whole organization or on certain parts alone, and indirectly by affecting the reproductive system.[27]

In looking at many small points of differences between species, which, as far as our ignorance permits us to judge, seem quite unimportant, we must not forget that climate, food, etc., have no doubt produced some direct effect.[28]

In all cases, there are two factors, the nature of the organism, which is much the most important of the two, and the nature of the conditions. The direct action of changed conditions leads to definite or indefinite results. In the latter case, the organization seems to become plastic and we have much fluctuating variability. In the former case, the nature of the organism is such that it yields readily when subjected to certain conditions, and all or nearly all the individuals become modified in the same way. It is very difficult to decide how far changed conditions, such as climate, food, etc., have acted in a definite manner. There is reason to believe that in the course of time the effects have been greater than can be proved by clear evidence.[29]

The greatest mistake I made was, I now think, I did not attach sufficient weight to the direct influence of food, climate, etc., quite independently of natural selection. When I wrote my book, and for some years later, I could not find good proof of the direct action (*i. e.*, in producing definite variations) of the environment upon the species. Such proofs are now plentiful.[30]

[27] "Origin," 1: 8.
[28] "Origin," 1: 104.
[29] "Origin," 1: 165.
[30] "Life and Letters," 3: 159, 1876.

DARWIN'S WORK ON MOVEMENT IN PLANTS

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IT is remarkable, when one considers the central interest of Darwin's life, that he should have found time and strength to devote so considerable a portion of his energy to purely botanical work. It is natural and fitting at this time that the major interest of the world should be directed to his larger achievements, but it should not be lost sight of that his botanical work alone represents no small labor accomplished. We may indeed not always agree at present with his conclusions and may differ even as to actual observations, but the fact remains that he developed a number of highly important topics relating to plant behavior.

His lines of investigation among plants were indeed somewhat special, for he made no pretence of covering completely the field of even that side of botany which interested him, but simply investigated certain more or less important phases of plant life that came under his notice. It may be expressed, perhaps, by saying that his botanical studies were his avocation, and were employed by him in a measure as a recreation from the exactions exercised by his larger tasks. That does not mean, however, that there was anything dilettantish in the spirit of his attack on botanical problems or that his work along these lines was not as thorough as his circumstances permitted. Thoroughness indeed was an important element in all that Darwin undertook and the patient application to even small details is the secret of much of the value of these botanical studies.

From his published letters it would seem that his work with plants was to him of the nature of a pastime, serious indeed but none the less a pastime, in which he often found himself so interested that all other lines of

intellectual activity were for the time forgotten. Possibly what first inclined him to study plants was the delight of observation and experiment to which he so keenly reacted, for, placed as he was in the country and in none too good health, these faculties found their easiest and most natural outlet in his garden. Even when he was least well, so long as he was able to exert any effort at all, his plants claimed his interest and one of his friends speaks of how in the daily walk about the garden path there was always some experiment or some particular plant which was to be watched and noted.

He did not himself make any claim to being a trained botanist and, without in any way reflecting upon the value of the work which he did, it must be admitted that he was not. He freely asked help of his botanical friends and freely it was given.

Most of his botanical contributions were published in book form and it is to be noted that they had a relatively wide circulation for books of a special character, a fact which speaks well for the manner of treatment and general interest of the subjects about which he wrote. Of these works there are three which especially concern the subject of this address and these are as follows: "Insectivorous Plants" published in 1875, "The Movements and Habits of Climbing Plants" which appeared first in 1865 in the *Journal of the Linnean Society* and was afterwards printed in book form, and "The Power of Movements in Plants" which bears the date of 1880. It is not the intention to take these up seriatim or discuss each detail, but rather to point out what seem some of the more important and crucial aspects of the various subjects treated therein.

Perhaps the most important single fact that Darwin elucidated was that of the universality of the oscillations of the growing points of plant members. This he termed circumnutation, a word now generally adopted; and by it he meant the swinging motion of plant extremities as they progress through space, due to inequalities of

growth. He was not indeed the first to observe individual instances of either periodic or ephemeral movements of a more or less pronounced degree, but to him belongs the credit of first insisting upon the fact that all growing organs describe a more or less spiral orbit. He developed this idea with such enthusiasm that he carried his line of thought to extremes and concluded that all plant movements were but modifications and adaptations of circumnutatory motions. Only in the cases of the motions of Mimosa leaves and Drosera tentacles did he express his doubt as to the applicability of the principle of circumnutation to all plant movements. He included all forms of tropisms, contact responses, other than those named, under this one head. In the final chapter of "The Power of Movement in Plants" he says:

> It has been shown that the following classes of movement all arise from modified circumnutation, which is omnipresent whilst growth lasts, and after growth has ceased, whenever pulvini are present. These classes of movement consist of those due to epinasty and hyponasty,—those proper to climbing plants, commonly called revolving nutation, the nyctitropic or sleep movements of leaves and cotyledons, and the two immense classes of movement excited by light and gravitation.

In the next paragraph he excepts the contact movements of Mimosa and Drosera, already referred to, saying:

> Although so many movements have arisen through modified circumnutation, there are others which appear to have a quite independent origin; but they do not form large or important classes.

When we consider the nature of the man and reflect that the whole trend of his mind was towards the concept of unity in the organic world it does not seem extraordinary that he should have taken such an attitude; an attitude too that was helped on by the extreme simplicity of his methods of experimentation. The very fact that he approached the question with a mind entirely free from bias had its advantages, but it also brought a greater chance of being too easily swayed by his own point of view. It must be remembered also that the distinction be-

tween autonomous and induced or paratonic movements was not so sharply drawn then as it is now. At present we place the tropistic movements due to whatsoever external cause, under the general class of aitonomic movements, in contradistinction to circumnutation, epinasty, hyponasty and so forth, which we are pleased to term autonomic or due to internal causes. In the latter class, it must be confessed, the relegation of movements to autonomous causes is often a mere confession of ignorance, as is well instanced by the older opinion first advanced by Darwin that the twining of stem climbers is wholly autonomic. It is only in the sense that the movements of fixed plant organs are in the vast majority of cases ultimately due to unequal growth changes that we can say that circumnutation is the fundamental process concerned. In other words, it is only if we were to define circumnutation as the power of plant parts to show either unequal turgescence or unequal growth that we could accept the universality of Darwin's statement.

As far as his observations on circumnutation proper are concerned, or, as he would have termed it, unmodified circumnutation, his conclusions are of the highest value, and form even to the present day really a large part of our literature on the subject. By the simplest means he plotted the orbits, so to say, of a very considerable number of growing tips. Entirely aside from any especial interpretation to be placed upon them, his descriptions of the behavior of seeds during germination and of the growth of seedlings, give a clear and accurate account of the general organography of the adolescent plant.

In another very important direction were the researches of Darwin rewarded by far-reaching results; namely, in the matter of the transmission of stimulus in plants. Until the publication of his experiments it had been largely overlooked that there might be a separation in space between the percipient and motor zone in tropic responses. It is true, no doubt, that some of his methods

and even some of his conclusions were faulty, but nevertheless the credit belongs to him for establishing a point of departure from which further developments of first importance have come. The demonstration of so fundamental a fact has had no inconsiderable influence in the understanding and interpretation of sense perception among plants.

Although many observers at first contended against the possibility of such a propagation of stimulus and denied the accuracy of Darwin's results, yet the general correctness of his statements has been established even though differences in interpretation may have crept in. One reason, no doubt, why it was difficult to admit and support Darwin's conception and to corroborate his results, is that the region capable of perceiving a stimulus is so localized and the conduction to the responsive area is over so short a distance. One may gather from his writings that he did not regard the response to stimuli in the nature of a release of a regulatory mechanism, as it is now so commonly understood: his point of view indeed as to the nature of such tropic responses as being merely a modified form of circumnutation was against such an interpretation. His attitude was of course that of the teleologist, for he was ever keen to uncover purpose in the reaction of organisms. In his concluding remarks and summaries, while he suggested the interpretation of such responses along the line of consciousness he exhibited a considerable reserve and went no farther than indicating the appropriateness of a comparison of the similarity to the responses in lower animals. He did not enter largely into the somewhat fruitless field of the philosophical discussion of the question. His reserve possibly but reflects the greater caution of a past generation in interpreting protoplasmic response universally in terms of what we know about the problem in higher animal forms, but be that as it may, one is inclined to the opinion that it was Darwin's own reluctance to commit himself too unreservedly which restrained him, for in

other matters he has amply shown that he was not afraid to combat what to him were mere conventionalities.

A large portion of his book on climbing plants is devoted to a consideration of the tendril bearers and takes up a wide range of forms. The exceeding sensitiveness of these organs to contact Darwin was one of the first to appreciate, but he went somewhat astray in supposing that mere pressure was enough to induce the characteristic coiling response. It was not thoroughly understood until later that weight alone is not sufficient, but that the stimulus must involve some more intricate contact shock. He did not understand that the exciting body must have a certain degree of what one may call roughness and consequently he did not understand the inaction of tendrils to raindrops.

His conclusions did not wholly agree with the now accepted explanations of the nature of the response of tendrils but it inclined to the view that the rapid reply of incurving tendrils was primarily caused by turgor changes ultimately rendered permanent by growth. More recently it has again been claimed that the curvature is wholly a growth phenomenon, but in so much as turgor changes are often apparently so greatly concerned with the first stages of cell enlargement incident upon growth, may not the initial curvature be after all a matter of unequal turgor pressure on the two sides of the tendril? Here as in other places Darwin considered the response of contact stimulus a form of modified nutation.

Although Drosera and similar plants were not considered by Darwin in this connection, in so much as some phases of his study had to do with their response to contact irritation, it is suitable to introduce the matter now. His investigation of the behavior of Drosera was especially detailed and represented at the time a great advance in the knowledge of the habits of this insectivorous form. There is not, as a matter of fact, any more elaborate or complete study at present, although his results were published some thirty years ago. Many important

observations were made by him, especially that the gland at the tip of a tentacle is exclusively the sensitive region and that a stimulus can be propagated down the central tentacles and along to and up the adjacent ones. Although he made most careful and repeated examination of the protoplasmic behavior as the stimulus progressed, and noted some curious changes which take place in the protoplasm of the responding tentacles, yet he was unable to advance any explanation of the physics of the process. Indeed, none has been offered since and much that Darwin said is still the last word on the subject.

Extending his work from the effect of mechanical stimuli to chemical ones, Darwin showed that many substances of very various kinds could effect a very vigorous response. He was, indeed, the first to make an endeavor at a close study of the insectivorous or rather carnivorous plants. Not only were his observations on the inflection of the tentacles of Drosera and the trapping of insects by this and other forms largely new; but also, and what was more important, perhaps, his investigations into the digestive action of their secretions were really the first in the field. His experiments along this line were especially exhaustive; and, with the exception of some details later writers have done little by way of correction or amendment. He did not it is true, isolate any specific enzymes but nevertheless we came to the conclusion that a pepsin-like enzyme was excreted by these plants, which enables them to digest external proteid material. He also noted the rennet-like action of the excretion in Drosera and arrived at the just conclusion that the curdling of milk due to the latter could not come from the acidity of the excretion alone, though at that time little or nothing was known concerning vegetable rennets. It is not to be wondered, when one considers the lesser acquaintance which was then possessed of ferments in general and plant enzymes in particular, that Darwin did not further discuss or attempt to investigate the enzymes which he had discovered and to determine whether they

were peptic or tryptic or whether the curdling power was due to a specific enzyme, apart from the others.

The complexity of ferment action and the possible co-existence of several distinct enzymes in one secretion was not fully appreciated at that time, and working as Darwin of necessity did, he was not in close enough touch with these matters as they then stood to branch out on his own account into very new fields. What he did do was to make a careful and pretty exhaustive empirical study of the action of the excretion of the glands on a great range of substances. If his list of the latter included a number which were immaterial by way of affording new light on the question and a few which, owing to their mode of preparation, gave inconclusive or erroneous results, it matters very little. He proved successfully the main thesis which he maintained, namely, the ability of these insectivorous plants to avail themselves of proteids as food. When one considers how much even to-day in the study of enzymes depends on almost pure empiricism and what valuable results have in the past been obtained by such methods, one does not cavil at Darwin's mode of attack, although at times it may impress one as a bit happy-go-lucky.

As a detailed study of the habits of an organism his extended observations on Drosera stand out as a masterpiece of this kind of work and the collective result of this work may justly be regarded as one of his best pieces of botanical investigation. It is evident from his letters that he took the keenest interest in this plant, which apparently stimulated his imagination and his desire towards investigation as much as any one thing which came under his notice. It was a subject peculiarly well fitted for his type of investigation, for in it he did not require elaborate mechanical aid to arrive at important results and the previous literature on the subject was scanty and for the most part of minor importance. He had an almost clear field and made the most of his opportunity by producing a work which must for all time re-

main the basis of our knowledge of these interesting forms. He pushed it as far as his means at hand permitted, and while in many points he could not arrive at definite conclusions, it is a fact that most of his unanswered questions are unanswered still. While his knowledge of plant physiology may not have been broad enough for him to correlate this special form of nutrition, with the general problems of plant metabolism it is to be remembered that after all it was not from such a standpoint that he took up the problem.

There is one characteristic which is particularly admirable in all of Darwin's botanical work and that was his endeavor in so far as he could to examine an abundance of different forms which would illustrate any topic under investigation. This is the more to be remarked since he was not really very fortunately placed in the matter of obtaining material. For keeping his plants after he had obtained them he had to depend entirely upon such facilities as his own garden and greenhouse afforded. Being unable himself to collect material to any extent, he had to depend upon the generosity of his friends and correspondents, who, it may be said, responded with alacrity. None but one of very active mind and great perseverance would have accomplished what he did in an experimental way under the difficulties which beset him, and his work affords a good example of how a relatively large amount can be accomplished by even a little time given continuously. Entirely aside from any absolute value which these books may have, they were an important contribution at that stage in the development of plant physiology, to the literature on the subjects on which they touched. No man with a less well developed faculty for detail and continued effort could have kept the thread of the work so well, despite the many interruptions to which it was subjected. Their value, it may be said, is more to botanical science than a merely sentimental one—it is rather in many respects one of real achievement.

It has been stated that one of the greatest services rendered by Darwin to the study of natural history was the revival of teleology. The presence of this mode of thought in his work shows no better anywhere than in his work on the movements of plants, where it apparently afforded to him one of his liveliest interests. In the light of the present disfavor into which teleological interpretations have fallen these statements, which are indeed in accord with the mental attitude of Darwin, require some comment. It is not that one need raise one's voice in favor of teleology as such, to apologize for his purposeful explanations of the form and function of organs; but it should in justice be said that it is where teleological evidence and teleological reasoning are accepted as a finality or where they lead to prejudgment that the most mischief is done. Darwin's whole make-up and trend of thought was such as to make him turn to immediate causal explanations for natural phenomena and he unquestionably was a teleologist, but in the main his interpretations were tempered by common sense, intellectual reserve and balanced judgment. It has been rightly said, too, that his teleology had a far wider and more coherent plan than that of his predecessors and it may be added it was less positive than that of some of his contemporaries and some of those that followed him.

It is wholly natural that with a mind like his, which ranks him with the greatest correlaters and unifiers of loose facts that the world has known he should also have attempted to unify the explanations of the phenomena examined in his botanical researches and his position as to the fundamental nature of circumnutation was no doubt a result of his temperamental attitude towards large questions. But while we need not necessarily follow him in all of his generalizations the fact remains that he did no inconsiderable service to botanical science if in no other way than, at least, in showing what may be learned from the close and careful examination of the plant as a living organism.

In a final summing up of Darwin's studies that have come under discussion here, perhaps a fair statement may be made by saying that he investigated, as accurately as both his knowledge and his facilities for experimentation allowed, a large range of plant forms which illustrated the especial subjects in which he was interested; that he discovered or drew attention to many important facts, either previously unknown or neglected regarding the habits of the plant forms which he had under observation; that if his interpretations were at times faulty, his observations were in the main accurate; and that he revivified subjects which had often times become only of more or less academic interest. Darwin himself—none better—recognized that many of his experiments must be unsatisfactory and his explanations merely tentative; and he was ready enough to accept correction which appeared to him justified. The very fact that he brought to his botanical researches a mind fresh and unprejudiced lends a peculiar value to his work. Unhampered by tradition and with an open mind, he interpreted the facts as he saw them, and we must remember that some of our criticisms may be in part due merely to the greater complexity of our own interpretations, than to any absolute superiority of them. Despite the advances which have been made, it should not be forgotten that Darwin's influence was in the direction of sound investigation; and we should not pass over ungratefully this phase of plant physiology from which has come much that is of the first importance to-day. As a stimulus to later investigators Darwin's work, whether in botany alone or in other fields, has had a profound influence on the plant physiologist though he may not always recognize it. It would be our shame if we could not have improved over the concepts of the science as current in Darwin's time, and our misfortune if we think that these betterments are not capable of as relatively great advance in the future.

AN EXAMINATION OF DARWIN'S "ORIGIN OF SPECIES" IN THE LIGHT OF RECENT OBSERVATIONS AND EXPERIMENTS

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ABOUT three years ago, some members of a local club, to which the writer belongs, having heard that Darwinism was on its death-bed, a report on the origin of species was ordered. The present paper is made up from notes prepared for that occasion.

In a letter to Hooker, March 9, 1885, Professor Huxley says:

> I have been reading . . . the book [Origin of Species] for the nth time. . . . It is one of the hardest books to understand thoroughly that I know of, and I suppose that is the reason even people like Romanes get so hopelessly wrong. ("Life and Letters," II, 204.)

If Huxley, who helped to fight Darwin's battles when "The Origin of Species" was young, who talked and argued with its author, can make such a statement concerning the book, it is little wonder that people come to different conclusions after reading it now.

My examination of Darwin's great work in the light of present-day beliefs has resulted in the finding of numerous passages which support the following theses:

1. Darwin's main thesis is the doctrine of descent as against the theory of the immutability of species.

2. A secondary thesis accounts for the origin of species by the theory of descent with modification through variation and natural selection.

3. Two kinds of variations are recognized: (*a*) Fluctuating variations as now understood, but including also variations of such a degree as would make steps in development as great as those which separate existing varieties. (*b*) Sudden changes, or sports.

It is to be observed that this classification of varieties

is not quite in agreement with the present-day distinction between fluctuating variations and mutations. Indeed, there are many who think that the distinction between the ampler fluctuations, on the one hand, and the lesser mutations, on the other, is not entirely established.

Darwin nowhere claims that natural selection is of the nature of a creative force.

I shall now cite a few passages in support of the above findings. References are made to the sixth edition. All italics are mine.

I. The main thesis is the origin of species by descent as opposed to the theory of the immutability of species or the independent creation of species.

While Darwin believed that varieties are incipient species he also believed that this identity had not yet been demonstrated. In speaking of the resemblance of varieties to species he says:

> Independently of the question of fertility and sterility, in all other respects there seems to be a general and close similarity in the offspring of crossed species and of crossed varieties. If we look at species as having been specially created, and at varieties as having been produced by secondary laws this similarity would be an astonishing fact. But it harmonizes perfectly with the view that there is no essential difference between species and varieties (pp. 261–2).

Again:

> It has been asserted over and over again by writers who believe in the immutability of species that geology yields no linking forms (p. 208).

And on page 290:

> Let us now see whether the several facts and laws relating to the geological succession of organic beings accord best with the common view of the immutability of species, or with that of their slow and gradual modification through variation and natural selection.

Also:

> This grand fact of the grouping of all organic beings under what is called the natural system is utterly inexplicable on the theory of creation (p. 413).

A few pages farther on he says:

> If species be only well-marked and permanent varieties, we can at

once see why their crossed offspring should follow the same complex laws in their degrees and kinds of resemblance to their parents, . . . as do the crossed offspring of acknowledged varieties. This similarity would be a strange fact if species had been independently created and varieties had been produced through secondary laws (p. 417).

On the following pages, 418–419, he summarizes facts such as the close resemblance between existing and extinct forms on the several continents, the inhabitants of oceanic islands, on islands near continents, and closes with this sentence:

Such cases as the presence of peculiar species of bats on oceanic islands and the absence of all other terrestrial mammals, are facts utterly inexplicable on the theory of independent acts of creation.

I make but one more quotation in this connection. Near the end of the book, in a sentence which the careless reader might understand to refer to something like the modern mutation theory, he says:

Under a scientific point of view, and as leading to further investigation, but little advantage is gained by believing that new forms are suddenly developed in an inexplicable manner from *old and widely different forms,* over the old belief in the creation of species from the dust of the earth (p. 424).

Such quotations could be multiplied many times, for over and over again throughout the book he speaks of his theory as standing for the mutability of species as against the independent creation of species. Indeed, so convincing to the world was Darwin's argument in support of his main thesis that the word Darwinism to the popular mind stands for the theory of descent, as it is perfectly right that it should do.

II. A secondary thesis is an attempt to account for the origin of species by the theory of descent with modification through variation and natural selection.

I shall now attempt to show by quotations:

1. Darwin's view of the part played by fluctuating variations.
2. The rôle of sudden variations.
3. The part taken by natural selection.

1. The following quotations would prove a narrow and

restricted meaning for the theory of descent with modification through variation if it were clear that Darwin always meant fluctuating variation when he used the word variation.

On page 156 he says:

> Why should not nature take a sudden leap from structure to structure? On the theory of natural selection we can clearly understand why she should not; for natural selection selects only by taking advantage of slight successive variations; she can never take a great and sudden leap, but must advance by *short and sure, though slow steps.*

In attempting to explain the puzzling phenomenon of the so-called neuter, really undeveloped female animals, he says:

> As natural selection acts only by the accumulation of slight modification of structure or instinct, each profitable to the individual under its conditions of life, it may reasonably be asked, how a long and gradual succession of modified architectural instincts, all tending towards the present perfect plan of construction, could have profited the progenitors of the hive-bee?

The answer to this query, by the way, begins with a sentence which has a very modern sound:

> This difficulty, though appearing insuperable, is lessened, or, as I believe, disappears, when it is remembered that *selection may be applied to the family, as well as to the individual, and may thus gain the desired end* (pp. 229–230).

The following utterance should be read with Darwin's main thesis in mind:

> If numerous species belonging to the same genera or families have really started into life at once the fact would be fatal to the theory of evolution through natural selection (p. 280).

Inferences have been drawn from the foregoing sentence as though Darwin had written: If numerous species, etc., have really started into life by variations greater than fluctuating variations, as that term will be understood at the beginning of the twentieth century, the fact would be fatal to the theory of evolution through natural selection.

Although, in his concluding chapter he makes use of such expression as:

. . . Complex organs . . . have been perfected . . . by the accumulation of innumerable slight variations.

He also says:

It is, no doubt, extremely difficult to conjecture by what *gradations* many structures have been perfected . . . (p. 404).

Again, on pp. 413–414:

As natural selection acts solely by accumulating slight successive, favorable variations, it can produce no great or sudden modifications; *it can act only by short and slow steps.*

I think that it is evident from Darwin's discussion of varieties of oaks that he would not have regarded such work as that of DeVries on the evening primrose as making a revision of the foregoing sentence necessary. Even if DeVries's mutants are what he thinks them to be, that is, elementary species, still evolution of species by that means must be by "short, slow steps."

Even if it should be shown that species originate only by mutation, the following sentence might be permitted to stand:

New species have come on the stage slowly and at successive intervals, and the amount of change after equal intervals of time, is widely different in different groups (p. 417).

2. By the following quotations I shall attempt to show the rôle which that kind of variation, now called mutation, plays in the evolution of species according to Darwin's view.

When it is noted that DeVries makes use of facts recorded by Darwin in support of his views, it will be seen that there is some reason for suspecting that some of the facts which in Darwin's day were thought to be of the grade of fluctuating variations were really of the kind now believed by many to be something quite different.

On page 22 is this statement:

Some varieties useful to him (man) have probably *arisen suddenly, or by a step.*

Examples are cited, *e. g.*, the fuller's teasel, the turnspit dog, etc. DeCandolle's memoir on the oaks of the

world is alluded to. This gives the rank of species to the forms which differ by characters never varying on the same tree and never found connected by intermediate states. Out of 300 species at least two thirds are provisional species. Thus *Quercus robur* has twenty-eight varieties, all of which, excepting six, are clustered round three subspecies.

Commenting on this condition of things, that is, where there is no clear line of demarcation between species and subspecies, and between subspecies and varieties, or between lesser varieties and individual differences, he thus concludes:

> Hence I look at individual differences, though of small interest to the systematist, as of the highest importance to us, as being the first steps towards such slight varieties as are barely thought worth recording in works on natural history, and I look on varieties which are in any degree more distinct and permanent, as steps towards more strongly-marked and permanent varieties; and at the latter as leading to subspecies, and then to species (pp. 41–2).
>
> A well marked variety may therefore be called an incipient species; but whether this belief is justifiable must be judged by the weight of the various facts and considerations to be given throughout this work (p. 42).

Darwin noticed that wide-ranging, much-diffused and common species vary most; also that species of the larger genera in each country vary more frequently than the species of the smaller genera; further, that many of the species included within the larger genera resemble varieties in being very closely, but unequally related to each other, and in having restricted range (pp. 42–45).

The following sentence is interesting in this connection:

> Every one who believes in slow and gradual evolution, will of course admit, that *specific characters may have been as abrupt and as great as any single variation which we meet with under nature or even under domestication.*

The above-quoted sentence follows a notice of Mivart's belief that new species manifest themselves with suddenness and by modifications beginning at once, of which Darwin says:

> This view, which implies great breaks or discontinuity in the series, appears to me to be improbable in the highest degree (p. 201).

Such statements appear to be contradictory, until it is remembered that the kind of new species meant by Mivart would involve such violently sudden changes as the three-toed Hipparion giving rise immediately to the one-toed horse; or the wing of a bird suddenly appearing in place of the fore-limb of some dinosaur.

Indeed, it seems to be to be demonstrable that the statement of Darwin's views respecting variation requires but little change to bring them into harmony, or, at least, make them include, the origin of varieties by mutation.

By abrupt variations which are yet not greater than a single variety may show, he means such cases as the six-fingered Kelleia family, or the ancon ram. It is of this kind he is speaking when he says:

> Excluding such cases of abrupt variations, the few which remain would at best constitute, if found in a state of nature, doubtful species, closely related to their parental types.

On the other hand, it is clear that he included under ordinary variations some, at least, which may now be called mutations. Thus:

> Although very many *species have almost certainly been produced by steps not greater than those separating fine varieties;* yet it may be maintained that some have been developed in a different and abrupt manner. Such admission, however, ought not to be made without strong evidence being assigned (p. 203).

This is probably as good a place as any to call attention to the fact that in the title of the book the theory is not stated to be the origin of species by the natural selection of favored *individuals,* but by the natural selection of favored *races.* Morgan's term *the survival of species* does not appear to me to be any improvement on this. To my mind a still better statement is that which stands at the head of a syllabus of lectures by Professor James D. Dana, "On the Theory of the Origin of Species through Natural Causes."

Resuming the citations, the following explicit statement is illuminating:

By the theory of natural selection all living species have been connected with the parent species of each genus, *by differences not greater than we see between the natural and domestic varieties* of the same species at the present day; and those parent species now generally extinct, have in their turn been similarly connected with more ancient forms; and so on backwards always converging to the common ancestor of each great class (p. 266).

Here is a sentence which anticipates some recent speculations respecting a so-called plastic period in the life of a species:

It is a more important consideration, leading to the same result, as lately insisted on by Dr. Falconer, namely, that the period *during which each species underwent modification,* though long as measured by years, was probably short in comparison with that *during which it remained without undergoing change* (p. 279).

To the same purport is the following:

This gradual increase in number of the species of a group is strictly conformable with the theory, for the species of the same genus and the genera of the same family, can increase only slowly and progressively . . . *one species first giving rise to two or three varieties,* these being slowly converted into species, which in turn produce by equally slow *steps* other varieties and species . . . (p. 293).

Concerning the origin of varieties he has this to say:

The complex and little known laws governing the production of varieties are the same, so far as we can judge, with the laws which have governed the production of distinct species (p. 415).

In the following passage provision appears to be made for the origin of varieties by mutation:

I have now recapitulated the facts and considerations which have thoroughly convinced me that species have been modified, during a long course of descent. This has been effected chiefly through natural selection of numerous successive, slight favorable variations; aided in an important manner by the inherited effects of the use and disuse of parts, and in an important manner, that is in relation to adaptive structure, whether past or present, by the direct action of external conditions, *and by variations which seem to us in our ignorance to arise spontaneously.* It appears that I formerly underrated the frequency and value of these latter forms of variation, as leading to permanent modifications of structure independently of natural selection, . . .

He adds, in answer to certain recent criticisms that he placed at the end of the introduction to his first edition, the following words:

I am convinced that natural selection has been the main but not the exclusive means of modification (p. 421).

3. The following explicit statement makes it very clear that Darwin did not regard natural selection in the light of an originating cause:

Some have imagined that natural selection induces variability, whereas it implies only the preservation of such variations as arise and are beneficial to the being under its conditions of life (p. 63).

It would appear that Huxley, in 1860, thought that natural selection was being urged as an originating cause. He says:

It is not absolutely proven that a group of animals having all the characters exhibited by a species in Nature has ever been originated by natural selection, whether artificial or natural.

He also thought that Darwin embarrassed himself by the use of the aphorism, *natura non facit saltum;* that nature does make a jump now and then, and that a recognition of the fact is of no small importance in disposing of many minor objections to the doctrine of transmutation. In 1861, in a letter to Hooker, he says:

The great desideratum for the species question at present seems to me to be the determination of the law of variation. . . . Why does not somebody go to work experimentally, and get at the law of variation for some one species of plant?

In 1885 he was reading the "Origin of Species" and finding it one of the hardest books to understand that he knew. In 1888 he says in a letter to Hooker:

Darwin has left the causes of variation and the question whether it is limited or directed by external conditions perfectly open.

Writing to Bateson, February 20, 1894 (?), he says:

I see you are inclined to advocate the possibility of considerable "saltus" on the part of Dame Nature in her variations. I always took the same view, much to Mr. Darwin's disgust, and we used often to debate it.

In the light afforded by these comments of Huxley, and after a careful rereading of the "Origin of Species," I am inclined to the belief that in the brilliant work of Hugo DeVries we may have a key to a real understanding of the difficulties in question.

Huxley, with his tendency to reach conclusions quickly, which, he confesses, sometimes led him into mistakes, saw intuitively, let us say, that the beginning of varietal differences might be by a sudden leap. While Darwin, who reached conclusions only after careful examination of all possible contributing data, although realizing that the origin of species from variations, by natural selection had not been proved, thought that they furnished the most favorable material for natural selection to work upon. At the same time, I think that I have shown by means of numerous quotations from the "Origin of Species" that the very slight changes which DeVries has shown to mark the beginning of some varieties, while recognized by Darwin, were thought of by him as of the same order as ordinary (now called fluctuating) variations. This view is justified, I think, by his frequent use of the word *step*. Possibly this explains why Huxley found the book such a hard one to understand thoroughly. It also throws some light on the unsatisfactory condition in which Darwin is supposed to have left the question of the origin of varieties. To my mind, instead of this being a blemish on Darwin's work, as it seems to be held by some recent writers, it is, when the state of biological knowledge in his day is taken into account, in harmony with his known caution and sagacity. To blame him for not making a sharp distinction between fluctuating varieties and mutations would be like finding fault with Copernicus for not knowing what Kepler and Newton discovered, or criticizing Newton harshly because his theory of light left much for subsequent workers before the electro-magnetic theory was possible.

THE DISTINCTION BETWEEN DEVELOPMENT AND HEREDITY IN INBREEDING

DR. EDWARD M. EAST

THE CONNECTICUT AGRICULTURAL EXPERIMENT STATION

THERE is among animal breeders a tendency to frequent out-crossing as a preventive of a feared deterioration of the breed through inbreeding. This fear is of long standing, probably having arisen contemporary with, or as a result of, the repugnance to incest possessed by so many human tribes. This general state of mind on the ethical question has brought about an unwarranted belief that there is a physiological law opposed to inbreeding *per se*. Inbreeding undoubtedly results in many cases of deterioration, but the success of the few daring spirits that have inbred superior stock shows that the cases of deterioration were merely made possible by the course pursued, and were not its direct and constant result.

In the vegetable kingdom a slightly different state of affairs obtains. Some species thrive under inbreeding while others appear to deteriorate. Maize is reduced in vigor in one generation, so that the difference between selfed and crossed plants is noticeable in seedlings two weeks old. Other natural species have evolved intricate mechanisms whereby they are perpetually self-fertilized, and some have even given up sexual reproduction for parthenogenesis (Taraxacum), and yet have survived in competition by their hardiness and prolificacy. Darwin even found that in species that generally appeared to be injured by inbreeding (*Ipomœa purpurea* and *Mimulus luteus*), individuals were occasionally produced that were not affected.

The classical researches which included the above observations are familiar to all. Direct comparison of crossed and selfed plants, and investigations into the mechanical means by which plants are cross-fertilized,

all pointed to the truth of the dictum "Nature abhors perpetual self-fertilization," which, by the way, simply corroborated the results that Knight had obtained a half century before. That there are important exceptions to this rule was recognized, however, and Hays,[1] arguing from the case of wheat, suggested that it be changed to read: "Nature abhors a radical change which would require species to cross in much closer or in much more radical relationship than is their long established habit." Each of these sayings is probably correct as far as it goes. Nature does seem to have provided more for cross-fertilization than self-fertilization. Yet the very fact that all species do not cross-fertilize naturally, shows that although cross-fertilization may be a desirable thing—a thing to be provided for by nature—it does not follow that inbreeding and decrease in vigor hold the relation of cause and effect because they are often linked together.

As a matter of fact, the data that we possess regarding the supposed degeneration through inbreeding do admit an entirely different explanation, an explanation more compatible with contemporary knowledge. The hypothesis, first suggested by Shull,[2] is that the danger from self-fertilization in naturally cross-bred species *may be due simply to the isolation of biotypes.* It is an established fact, although the cause is unknown, that crosses between nearly related types (in both animals and plants) are usually more vigorous than either of the parent types alone. Since inbreeding tends to isolate types homozygous in their characters, these homozygous types, coming from species naturally crossbred, are thus deprived of the stimulus which came through free intercrossing and appear to deteriorate.

A little later the present writer[3] pointed out that a

[1] Hays, W. M. "Plant Breeding." Bull. U. S. D. A. Div. Veg. Phy. & Path. 29: 1901.

[2] Shull, G. H. "The Composition of a Field of Maize." *Ann. Rpt. Amer. Breeders' Assn.* 4: 1908.

[3] East, E. M. "Inbreeding in Corn," Ann. Rpt. Conn. Agr. Exp. Station, 1907–8.

reconsideration of the work of Darwin and others shows that it accords with this theory. As a single example from Darwin we may consider the experiments with *Ipomœa purpurea,* which were his longest, being carried on as they were for ten generations. If an actual degeneration were taking place it might be expected that the difference in height between the crossed and the selfed plants should have gone on increasing in the later generations. Such was not the case, however, and Darwin himself remarked upon it. Nevertheless, the results obtained were what should have been expected by the hypothesis just given, for after a few generations even the crossed plants in such a small lot would have become more or less inbred, and would have approached the inbred stock in size. In further support of this view it is noticeable that the crossed flowers varied in color in the earlier generations, but became more uniform toward the end of the experiment, while the selfed plants were uniform in color throughout the whole time. This, then, explains why his out-crosses with other stock showed greater vigor than did cross-fertilization within a type, the latter strain having become more nearly identified with the selfed plants through continued close breeding.

Such results as the above from Darwin, my own experiments with maize and tobacco, together with the ready agreement of the facts in other breeding work with which I am familiar, indicate that this problem of degeneration combines two questions; the one a question of heredity, the other a question of development. Davenport[4] has recently called attention to what I consider the former question, suggesting that deterioration through inbreeding may be due to the isolation of homozygous recessives, or the combination of recessive di-hybrids. This is undoubtedly true when the allelomorphic pair under consideration is the presence and absence of something essential to the normal development of the organ-

[4] Davenport, C. B. "Degeneration, Albinism and Inbreeding." *Science,* N. S., 28: 454, 455, 1908.

ism. But the principle will probably be found to apply also where there is presence of an abnormal dominant character. We do not know many such characters at present, but susceptibility to rust in wheat and congenital cataract in man may be cited as approaching our meaning.

The instances where the presence or absence of evil qualities is brought to notice through their isolation by inbreeding are few in number, however, and can not account for the large number of cases where there is a loss of vigor by this means.

Let us consider just what this deterioration, so-called, is. Does it represent an actual degeneration in hereditary characters? In general it does not. Darwin's experiments consisted mainly in comparing heights of plants. His measure of vigor, then, is a measure of rapidity and amount of cell division. In no cases does he speak of losses of characters, and seldom of disease. Even where disease appeared, it usually appeared alike in inbred and cross-bred plants. In my own experiments, I have observed some twenty-five families of maize inbred for two generations, and a lesser number through the fourth generation, and have not found a single sign of degeneration. In all characters of stalk, leaves, roots, male inflorescence, female inflorescence, and mature seed, the plants were normal. It is merely in the matter of size of plant and ear, and thereby yield, that the plant compares unfavorably with cross-bred plants.

Further, there is no *continuous* decline in yield as should be expected in actual degeneration. There is somewhat greater difference between fourth generation inbred and cross-bred plants than there is between those of the second generation. This last fact may be explained by considering the frequency with which heterozygotes in certain characters are selected even in the most careful work. Not all character pairs can be kept under observation, and from the mere fact of its being inbred we can not presume that the isolation of a homozygous strain is complete. The past summer one of our

fourth-year inbred families was found to be heterozygous in the character pair presence and absence of color in the silk. But there is absolutely no indication that there is loss of vigor *after* the isolation of a homozygous individual.

It seems, then, that this type of degeneration (the common type) is limited to a partial loss of power of development, a reduction in rapidity and amount of cell division. The phenomenon is readily apparent in open fertilized plants like maize, for there the vigorous growing hybrids are continually being formed in nature. When the components of these hybrid strains are isolated by inbreeding, reduction in vigor is immediately seen. In plants like tobacco, which are naturally inbred, no degeneration is suspected, for the natural plants are taken as the standard. There is an increase in vigor, however, when inbred tobacco strains are crossed, and if the F_1 generation is then taken as a standard, there is a loss of vigor through inbreeding comparable to that which takes place in maize.

Upon what theoretical basis can these facts rest? In the first place, whether or not we accept the theory that the nucleus is the bearer of all hereditary characters, nevertheless we must believe that amphimixis has two functions, the one a recombination of hereditary characters, and the other a stimulation to development. If we postulate that there is an increase in this stimulation when two strains differing in gametic structure are combined, we satisfy all observed conditions. This will explain why *decrease in vigor* and not *degeneration of characters* is usually the sole effect of inbreeding, and will also show why this decrease must reach a limit with the complete isolation of an individual homozygous in all characters, and never will result in a complete degeneration, or "running out," of the strain. One other effect sometimes noticed in inbreeding is also thoroughly in accord with the hypothesis. This is decrease in fertility. Since fertility must necessarily start with the union of

the gametes and their subsequent division, a decrease in this stimulation in species which have for ages depended upon cross-fertilization may result in decreased fertility.

We can scarcely form a definite idea of the mechanism through which such a stimulation may take place. There may be chemical compounds found in different strains that react when brought together. If this were the case we should expect to find separate families with like "compounds" which when crossed would not be more vigorous than when inbred. It would be difficult to establish such a thing experimentally. On the other hand, the actual fact of difference[5] in gametic constitution may set up a biological "action" analogous to ionization. If this were true, and individuals of the F_1 generation heterozygous in all differentiating characters were selected in succeeding generations, there should be no reduction in vigor, while individuals of the F_2 generation, homozygous in their characters, should compare in vigor to the P_1 generation. This hypothesis we are testing, but results will necessarily be slow.

The F_1 generation of thirty maize crosses were grown in 1908 on well fertilized land in Connecticut. They were planted three feet six inches each way, about four stalks to the hill. Seeds from the same parent ears[6] which were used to make the crosses were also grown for comparison. Only fifty hills of each of the crosses and of each parent could be grown on account of limited space, but the soil conditions were such that a very fair

[5] The objection will be raised that beyond a certain amount of difference between gametes, there will be sterility. It is generally true that there is sterility with wide differences in botanical or zoological characters, but there are exceptions, and we must not fall into the same old rut of putting the two down as cause and effect because there is at present no other explanation. It is definitely settled that in certain cases the bar to fertility is merely the mechanical inability of the spermatazoon to penetrate the ovum. It seems reasonable that the stimulation effect may be illustrated by borrowing Galton's polyhedron.

[6] The parent ears were, therefore, one year older, but their germination was good, and their growth equal to inbred seed of the same ages as the hybrid seed.

indication of the comparative vigor of each strain was obtained. Unfortunately crows and chipmunks played havoc with the "stand" in a number of cases, and accurate figures can not be given except in the following four cases where the stand was perfect.

A white dent no. 8 yielded 121 bushels per acre (at 70 pounds per bushel); a yellow dent no. 7, which had been inbred artificially for three years, yielded 62 bushels per acre; the cross between the two varieties, no. 7 ♀ × no. 8 ♂, yielded 142 bushels per acre.

Longfellow, no. 34, an eight-rowed, yellow flint yielding 72 bushels per acre, was crossed with the same no. 8 white dent, yielding 121 bushels per acre; the resulting cross yielded 124 bushels per acre.

Sturges's hybrid, a twelve-rowed, yellow flint with a tall, non-branching stalk partaking of the characters of dent varieties, was also crossed with no. 8 white dent. The flint parent yielded 48 bushels per acre, while the cross yielded 130 bushels per acre.

Two families of a yellow dent variety, which had each been inbred artificially for three years, were the parents of the fourth cross. No. 12, yielding 65 bushels per acre, was crossed with no. 7, yielding 62 bushels per acre. The F_1 generation yielded 202 bushels per acre. This last result is somewhat distorted, as five stalks per hill of the cross were allowed to grow while of the parents only four seeds per hill were planted. About 90 per cent. of the seeds produced mature stalks. Notwithstanding the closeness of planting to which this cross was subjected, however, casual observation was sufficient to show that it soared far beyond each parent in vigor of plant and size of ear.

In the remainder of the field every possible combination of dent, flint and sweet maize was grown, and in every case an increase in vigor over the parents was shown by the crosses. It is to be regretted that comparable yields could not be obtained in every instance, but, as a matter of fact, the differences were so apparent

to the eye that it is almost unnecessary. The figures presented do not show the average increase to be expected by a cross. The manuring was heavy, the cultivation intensive, and the yields were beyond the ordinary. But they do show that in practically every case a combination of two high-bred varieties of seed corn is more vigorous than either parent.

The importance of this fact in commercial corn growing is considerable, and is likely to increase in the future, for the following reason. The corn breeding methods in use vary as to detail, but their purpose is the same, namely, to produce high-yielding strains. The older idea was that continued selection of plus fluctuations would invariably yield results. At present, there are more adherents to the view that man can do more than isolate from the mixture of types we call a commercial variety the most perfect type that nature has produced in this variety. It is all line breeding, and as it is carried on on small plots, the tendency toward the production of an *inbred strain increases with the length of time the work is prosecuted.* Thus, unless new mutations intervene, chance of improvement is limited to the latent possibilities of the first breeding plot.

Shull[7] has already suggested that either definite recombination of previously isolated biotypes, or relaxation of selection after partial isolation and rejection of the less efficient biotypes, will be found to be the logical procedure in corn breeding.

The writer has become a convert to the first method

[7] Since this manuscript was sent to the printer the writer received from Dr. Shull, as a timely coincidence, a copy of a paper that he had read at the annual meeting of the American Breeders' Association, in January, 1909. In it he deals with a similar method of corn-breeding, namely, the actual isolation of homozygous strains by artificial inbreeding, and their recombination later. His method is more correct theoretically, but less practical than that of the writer. From this paper I inferred that his views must accord with the theory presented in this paper. Replies to my inquiries show that our ideas are strictly in harmony, although Dr. Shull had not treated the theoretical phase of the subject, having considered it as beyond the scope of his paper.

in a modified form, and suggests the following scheme. There must always be corn specialists to continue line breeding, and this method is not for the corn breeder, but the corn grower. The latter should purchase from the line breeder two strains of seed each year, and grow the F_1 generation of the cross between them.

The method requires a small isolated hybridization plot in addition to the commercial field. In this plot the two strains are planted in alternate rows. The male inflorescence is removed from one strain at flowering time and all of the seed for the commercial field selected from this crossed strain. Some hybrid combinations will be found to be more vigorous than others, but I am convinced that practically any cross within the subspecies will be profitable. Crosses between the subspecies, while more vigorous than the mean between the parents, have certain disadvantages, such as variation in the time of ripening, which make them less desirable for practical use.

BREEDING EXPERIMENTS WITH RATS

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The following experiments chiefly between the black and the roof rat were undertaken as one of a series to determine how far the Mendelian law of discontinuous inheritance applies to wild varieties and species. Most of the cases of Mendelian inheritance have been determined from domesticated forms in which the varieties seem to differ from each other in the loss of one or more characters. Until we know more about the results when wild varieties are crossed with their wild species or with other varieties, we can not safely apply Mendel's law to the process of evolution.

There are two species of house rats found in this country in addition to the common gray or Norway rat. One of these is the black rat, *Mus rattus,* that still exists in isolated communities in the north. It also infests, I believe, certain ports in the southern states and Central America.

The other, the roof rat or Alexandrian rat, is said to have been introduced from Mediterranean ports by ships. It is generally described as a variety of the black rat.[1] The roof rat is gray, it has the ticked or barred gray hair common to most wild rodents. It may, therefore, be looked upon as the original form from which the black rat has been derived. If this is the case we might expect to find that the gray color is the dominant one and the black the recessive, especially since in the domesticated species of the Norway rat, black is recessive to gray.

To my surprise I found that in the first generation the

[1] The black rats used in these experiments were obtained at Amherst, Mass., through the kindness of Mr. Clarence Birdseye. I am indebted to the Carnegie Station at the Tortugas and to Dr. Stockard and to Professor Edwin Linton for obtaining and transporting the roof rats used in these experiments.

hybrids are *black* whichever way the cross is made. Black is dominant to gray. In all I have thirty-two such individuals.[2] These black hybrids inbred have produced one litter of four black[3] and one gray. The numbers are too small to furnish conclusive data, but as far as they go they indicate that the two colors follow Mendel's law.

The roof rats are white below as is also the Norway rat, but there is a peculiar difference. In the roof rat the white hair is white to its very base, i. e., it is not ticked. In the Norway rat the ventral hair has a dark base as in most other rodents.

All attempts to cross the black rat or the roof rat with the Norway rat, or with its domesticated varieties have failed, although by putting young rats together I have had them live in harmony for a year or more. It would appear that the two species *M. decumanus* and *M. vattus* are infertile.

On the contrary as stated above *M. vattus* and *M. alexandrinus* are perfectly fertile inter se.

In respect to the ticking of the ventral hair it is interesting to note that spotted gray mice of the domesticated breeds have the hair of the white spots uncolored all the way to the base, as in the albino. I have found a wild species of brown mouse that has a white belly and the hair is ticked, i. e., it has a dark base. When such a mouse is crossed with a spotted mouse the first generation is gray with a white belly—the hair being ticked. Such mice inbred produce amongst other combinations some spotted mice. In these mice wherever a white spot extends down the sides and across the belly the region of the spot on the belly has hairs white to the base. In other words, the white spot dominates the white belly in the same way that it dominates the gray hair of the sides and back.

[2] There is some variation in the color of the black hybrids of the first generation. One that was reddish black at first later became black.

[3] In the second generation the four black individuals, still young, show some differences in the shades of black.

If the white belly of the roof rat turns out to be a character separable from the uniform gray coat, as I have found to be the case with white-bellied gray mice, we may expect to find in the second generation of hybrids some gray rats with a gray belly.

The chief point of theoretical interest in these results concerns the origin of the black color in the black rat. If it is produced by the loss of the ticking factor, as Castle suggests for other black rodents, it is inexplicable why the black should dominate when crossed with the ticked gray coat of the roof-rat. If, on the other hand, the rat has arisen by the black color spreading over and obscuring the ticking beneath, then we could understand how it dominates in the first generation; also why the result is different from that when the black variety of the Norway rat is crossed with a gray rat. It remains for further work to settle this point.

The common gray or Norway rat has, as stated, a white belly—the white hairs having a black base. When such a rat is bred to an albino having black (possibly gray also) as a latent character, the first generation contains only gray rats as Crampe and Doncaster have shown; but the color of the belly varies—a point that has hitherto escaped notice In some individuals the ventral hair is a slate-color, in others it is nearly white. In both the base of the hair is blackish. There appears to be an almost, perhaps a complete, gradation between white and slate-colored belly. The extremes may be accounted for as follows: The albino may carry black-bearing and gray-bearing germ cells. When the former unite with a gray-bearing germ cell of the gray Norway rat, the addition of black may cause the black base of the ventral hair to extend farther out towards the tip, making the belly slate-color. When a gray-bearing germ cell (of the albino) meets the gray-bearing germ cell of the albino, little or no change may take place in the ventral region.

Another interpretation is also possible. The albino may carry a uniform coat, *i. e.*, one that gives gray (or

slate) below instead of white. The presence of this condition may dominate in some of the first hybrids.

In addition to the points noted above it should be recorded that in nearly all of the individuals, resulting from a cross between a wild gray Norway rat and an albino, there occurs a pure white spot or streak on the belly, as other observers have recorded. The hair of these spots is white to its base. This result is obviously due to the incomplete dominance of the uniform coat. The albino in my experiments, carried, latent, not only black, but a spotted "condition," as the second generation demonstrated. The presence of this condition in the hybrids of the first generation is shown to the extent of the white ventral spot. This region of the body is, as it were, a "weak" area in which the recessive character displays itself, although elsewhere, as a rule, the spotting is suppressed. The result shows that at certain points in the pelage a recessive character may crop out in a dominant-recessive individual.

In the second generation gray, black, spotted gray, spotted black and albinos appear, as others have already shown. In the uniform gray individuals a series of types occur varying from rats with white bellies, like that of the wild gray rat, to those with a uniform slate-colored belly. The gray color itself is subject to some variation —the result depending perhaps on the condition of the black present.

SHORTER ARTICLES AND DISCUSSION

THE CHUB AND THE TEXAS HORN FLY

In the upper reaches of the waters of the Niobrara River, locally known as Running Water, the common chub, *Semotilus atromaculatus*, is very abundant. One may with a hook and line secure many dozens of them in a very short time. In Running Water they scarcely ever attain a greater length than eight inches. During the past summer while out on a collecting trip into the Miocene beds of northwestern Nebraska, some interesting observations were made on certain feeding habits of the chub which may prove of interest to those naturalists who are especially interested in animal behavior and intelligence.

The horn fly, *Hæmatobia serrata*, according to Kellogg, is a European insect which gets its popular name from the habit of clustering on the bases of the horns of cattle. It was first

introduced into this country about 1886 or 1887 and its spread has been so exceedingly rapid that in a very few years it has become an annoying pest to western cattle. Mr. James H. Cook, a prominent ranchman of Sioux County, Nebraska, told me that

he had never seen the horn flies so abundant as they were the past summer. They literally swarmed around the cattle and since the majority of the stock was dehorned the insects would settle all over the backs and sides of the animals although they were in some cases observed to cluster around the horn bases.

At Harris's ford, where the collecting parties crossed Running Water, several hundred cattle watered all summer. The lower part of the ford is quite shallow, scarcely attaining a depth of more than a foot; somewhat to the right the water deepened so that the cattle in drinking would be submerged nearly to the middle line of their bodies. At noon the cattle would begin to come to water and would continue coming for some hours on hot days; on cooler days they would delay their coming somewhat; and on rainy days they frequently did not come at all. The following observations were made on hot, bright days as our party was returning to camp from the morning work. Mr. Albert Thomson called my attention to the actions of the fishes and we together made the following observations repeatedly.

The cattle would almost always enter the stream at the shallow part of the ford and gradually wade up stream, drinking as they went, until they came to the deep place near the fence where the water reached well up on their bellies. The chubs seemed to be unusually numerous at the ford, and we often wondered at the great numbers of the little fishes which we could see in schools in the clear water. Their presence was soon explained. As soon as the cattle entered the stream at the shallow place in the ford the chubs would come out from their cool and shady retreats under the grasses along the sides of the bank and hasten to meet the cattle at the shallows. Often we saw as many as a dozen or more chubs following a single cow. As soon as the water came near the bellies of the animals the chubs would leap out of the water and catch the horn flies from the sides of the cattle. Often we saw them leap as much as half their length out of the water to secure a fly which was high up on the animal's side. These observations were made on several consecutive days, and on the last day but one I was so fortunate as to secure a photograph of a chub in the act of catching a fly from the side of a cow and the photograph is published herewith.

That the fishes actually learned that the dark spots on the sides of the cattle made good food, there can be no doubt. Just how they first learned it we may not know. The chubs had fur-

ther learned that the coming of the cattle meant food for them, hence they would meet the cattle in the shallows and follow them to deeper water. The act of these fishes leaping to secure flies from the sides of cattle is so unusual that it is deemed worthy of notice and it is hoped that the incident may be of service to those interested in animal behavior.

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NOTICE OF A NEW CAMEL FROM THE LOWER MIOCENE OF NEBRASKA

In the autumn of 1906, the writer found a nearly complete skeleton of a camel, in the Lower Harrison Beds, near Agate, Sioux County, Nebraska. The skeleton is finely preserved and articulated. It had apparently been washed into a heap while the muscles still held the bones together, for it is literally tied in knots. On this account it has only been partly removed from the matrix, and so a complete description is deferred.

The type (No. HC125, private collection of the writer) is an adult animal, and consists of a complete skull and jaws, a practically complete vertebral series, fore limbs and feet, pelvis, sacrum, and the greater portion of the hind limbs and feet. The latter were damaged by erosion. It is referred to the genus Oxydactylus, and the specific name of *Campestris* is proposed.

It is apparently closely related to *O. longipes*,[1] but is a much smaller and somewhat less specialized type. This seems the more natural when we remember that *O. longipes* was found in a somewhat later horizon. The skull in general contour is very similar to *O. longipes*, but exhibits some distinct features. The upper incisors are proportionally slightly larger than those of *O. longipes*, the third incisor being a little larger than the canine. The diastema separating these two teeth is relatively shorter than in the latter, and the facial portion of *O. campestris* is relatively shorter. The premaxillae are separated at the proximal extremity by an unusually large U-shaped opening, 8 mm. wide and 10 mm. long. P^2 and P^3 are slightly more robust in the present species. The limbs are long and slender, though much shorter than those of *O. longipes*. The metacarpals are entirely separate. On the sides of the proximal end

[1] *Annals of the Carnegie Museum*, Vol. II, No. 3, pp. 434–475, 1904.

of the metacarpals are small, flat, rugose bones, remnants of metacarpals II and V. When the specimen is entirely cleaned of the matrix, a more complete description will be given.

MEASUREMENTS

	O. campestris.	O. longipes.
Greatest length of skull	290 mm.	340 mm.
Length of diastema I^3 to canine	7 mm.	13 mm.
Length of diastema canine to P^1	12 mm.	14 mm.
Length of diastema P^1 to P^2	15 mm.	18 mm.
Lengtn of continuous molar-premolar series	88 mm.	102 mm.
Length of metacarpals	275 mm.	345 mm.
Length of proximal phalanx	51 mm.	66 mm.
Length of median phalanx	20 mm.	31 mm.
Breadth of metacarpals III and V	15 mm.	23 mm.

HAROLD JAMES COOK.

September 15, 1908.

NOTES AND LITERATURE

The Chondriosomes as Bearers of the Hereditary Qualities.—Meves, in a paper entitled, "Die Chondriosomen als Träger erblicher Anlagen"[1] presents a new and interesting view in regard to the bearer of the hereditary qualities. Since Hertwig, '75, reached the conclusion that fertilization consists in the union of male and female pronuclei, the nuclear theory of heredity has been criticized by many able investigators, and the new interpretation which Meves gives at this time indicates that many are still dissatisfied with the all-sufficiency of the theory, and are eagerly seeking and grasping, as it were, the first visible sign of any other substance which may serve to carry the hereditary qualities.

Meves finds in the chick embryo, between the second half of the first and the first half of the fourth day of incubation, by means of special fixing and staining reagents, a large number of independent threads, fibers, rods or granules. The shape of these structures varies in different cells and at different times in the same cell, although they are all one and the same substance. He concludes that these structures are identical with the "Cytomikrosomen" of la Valette St. George, the "Mitochondrien" of Benda and the "Chondriokonten" of Meves, and proposes to unite them under the term "Chondriosomen." He also believes that the granules of Altmann, except those produced by regents, are identical with the chondriosomes. They have been described by Benda, Meves and others in various tissue cells, plant cells and in sex cells. Benda, '03, suggested that possibly the mitochondria might play a rôle in heredity, and with this suggestion Meves agrees.

Nägeli's idioplasm hypothesis and many other similar theories have been advanced to account for heredity, but these have been criticized on the ground that they lack a material substratum, and that they are purely speculative. Meves believes that the "fantastic structure," as it was called by Sachs, has now become a reality in the chondriosomes. While Nägeli supposed the idioplasm to produce different differentiated products by

[1] *Archiv für Mikroscopische Anatomie und Entwicklungsgeschichte,* Bd. 72, 1908.

special activities on the surrounding cytoplasm, Meves believes that the differentiated parts arise by a direct metamorphosis of the chondriosomes.

Meves realizes that the nuclear substance answers fully the demands of a hereditary substance, namely, that in fertilization the two parts must be equivalent, that there must be a reduction, and that there must be an equal division in cleavage. However, he says that it has not been proved that the nuclear substance and hereditary substance are identical, or that the nuclear substance is the only hereditary substance. He then asks the question, how far do the chondriosomes satisfy conditions demanded of a hereditary substance. It is evident that the quantity of chondriosomes present in the egg cell is much greater than that brought in by the sperm. This fact, he says, presents no great difficulty, if we suppose that the specific qualities of the chondriosomes becomes expressed through the configuration of transverse sections. According to Nägeli, an over-supply of idioplasm may be thrown out from the idioplasmic system at the time of fertilization and become changed into yolk. In favor of this view Van der Stricht and his students have shown that a part of the mitochondria of the egg cell are changed into yolk granules.

There is also the possibility that the male chondriosomes, after entrance into the egg, multiply and divide. There is not an equal division of the chondriosomes in cell division, as there is of the chromatin, but they do approximate to equality of division and any difference may be made good by increased growth.

As there is a reduction of the chromatin before fertilization, Meves suggests that there may be a reduction of the chondriosomes. However, he has not seen even the slightest indication of a reduction, and until some evidence is forthcoming, such a suggestion must remain as a mere speculation. Duesberg, '07, has shown that there is a mass reduction of the chondriosomes in the two spermatocyte divisions, but in the egg this is not true, as the chondriosomes remain scattered throughout the cell, and the resulting cells are very unequal in size.

Meves suggests another way to prevent the increase in the hereditary mass, and this is as Nägeli has shown. Nägeli supposes the male and female idioplasm to unite as a mixed product. A cross section through the union of the embryonic strands shows that the idioplasm strands, in relation to the number of micellæ rows, remains unchanged. A paternal and maternal idioplasm

thread in fertilization, then, must unite end to end to form one of double length. While Meves ascribes a large part in the transportation of hereditary qualities to the chondriosomes, he does not claim that they alone, to the exclusion of the nucleus, carry these qualities. He thinks that both nucleus and cytoplasm work together, the qualities of the nucleus being carried by the chromosomes, those of the cytoplasm by the chondriosomes.

F. PAYNE.

Cultural Bed-Mutations in the Potato.—E. Heckel[1] has reared the white-flowered *Solanum maglia* from tubers received from Sutton and from Vilmovin. The young plants resembled perfectly typical *S. maglia.* They were transplanted from the greenhouse to a fertile garden where common potatoes had been grown the year previously. The tubers obtained differed greatly from those planted and those characteristic of this species. They weighed from ten to twenty times as much. One in particular weighed 135 grams; the flesh instead of being watery and slightly bitter as it typically is, was compact and full of starch—the tuber was edible. This tuber being planted gave, the next year, five tubers from 87 to 62 grams in weight. The other tubers (of smaller size) yielded tubers of from 50 to 5 grams—the smallest having the size of the typical tubers of *S. maglia.* The author refers to the large potato obtained by him from *S. maglia* as a mutation, but suspects that its size may have been influenced by the previous growth in the same soil of the common tubers.

[1] *Ann. des Faculté des Sci. Marseille,* XVI, 1907.